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# Patch identity and the spatial heterogeneity of woody encroachment in exotic-dominated old-field grasslands

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**Abstract** Most grassland communities in agricultural landscapes comprise a mix of exotic and native plants, where grasses and forbs are disposed in low diversity patches conforming a heterogeneous matrix of vegetation. Within these “novel” ecosystems, woody encroachment is one of the principal causes of ecosystem degradation. Here, we examined the resistance to exotic woody establishment (*Gleditsia triacanthos*) into four different monospecific patches characteristics of old-field grasslands in Inland Pampa: an annual forb (*Conium maculatum*), an annual grass (*Lolium multiflorum*), and two perennial grasses (*Cynodon dactylon* and *Festuca arundinacea*). We evaluated the filter to tree recruitment by rodent seed removal and survival and growth of *Gleditsia* seedlings transplanted into undisturbed and disturbed microsites, within each patch. Beneath intact vegetation seed removal was an important biotic filter to woody establishment whereas disturbances facilitated seed survival in patches of perennial grasses. Patch identity affected tree growth, and *Cynodon* reduced the final biomass compared to forbs. Disturbance enhanced tree performance independently of patch type. After 2 years, tree survival was independent of disturbance and patch identity. As patch identity may regulate granivory and growth of tree saplings, community susceptibility or resistance to woody invasion rather than representing a static community attribute could vary according to the dynamic changes in the proportion of susceptible-resistant patches. Broadly, our work reinforces the concept that mechanisms regulating vegetation heterogeneity add a component of stochasticity to biotic resistance to community plant invasion.

**Keywords** Pampean grasslands · Woody invasion · Seed predation · Seedling establishment · Competition · Novel ecosystems

## Introduction

Woody encroachment in grasslands is a worldwide phenomenon with major implications for conservation and ecosystems services provision (Briggs et al. 2005; Pejchar and Mooney 2009). Factors operating at different spatial and temporal scales have been advocated as triggers of invasion, including propagule pressure, recipient community characteristics, and disturbance regime (Levine et al. 2004; Lockwood et al. 2007; Davis et al. 2000; Bond 2008; Chaneton

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et al. 2012). In general, the approach employed to evaluate community resistance to plant invasion has considered communities as homogeneous well mixed species assemblages (Elton 1958; Lonsdale 1999; Theoharides and Dukes 2007). However, grasslands are frequently composed of a mosaic of low diversity or monospecific patches (Armesto et al. 1991; Tognetti et al. 2010), which in turn might differ in their susceptibility to woody encroachment. Therefore, incorporating fine scale patch interactions into the general framework of invasion may help to predict and manage community invasibility.

Plant invasions can be thought as a chain of processes including seed dispersal, plant establishment and growth, and population spread (Levine et al. 2004), which in turn produce direct and indirect effects on resident vegetation. Assuming successful seed arrival, seed consumption represents one of the first biotic filters to plant invasion when seed quantity is scarce (Crawley 1983; Lockwood et al. 2007) and/or when the invader seeds have higher nutritional quality than resident ones (Busch et al. 2012). At the community scale, the magnitude of granivory may vary according to habitat productivity and vegetation structure (Manson et al. 2001; Hodara and Busch 2010; Busch et al. 2012), while at the patch scale, microhabitat conditions associated with different patch types may attract or repel consumers (Hodara and Busch 2010; Garcia et al. 2011). As a consequence, some patches could provide shelter, others food and/or food and shelter while others could be avoided by consumers (De Steven 1991; Murillo et al. 2007). In general, patches dominated by species which accumulate large quantities of aerial biomass offer better shelter to seed consumers than patches dominated by species with low cover and biomass (Hodara and Busch 2010). Therefore, we expect higher seed consumption and lower opportunities to woody establishment in perennial patches. Conversely, canopy gaps represent high-risk microsites for consumers, thus disturbances should enhance the chance of tree establishment by lowering seed consumption (Fedriani and Manzaneda 2005).

In the subsequent invasion stages (Levine et al. 2004) diverse hypotheses have been postulated to explain community resistance to plant invasion (Richardson et al. 2001). In particular, the biotic resistance hypothesis asserts that interspecific interactions will be enough to repel plant invasion (Maron and Vilà 2001). However, while it is recognized that grasslands communities are organized as a mosaic of patches (Armesto et al. 1991), few studies have focused on the importance of spatial heterogeneity and fine scale interactions as relevant aspects of community invasibility (but see Jurena and Archer 2003; Davies et al. 2005; Tognetti and Chaneton 2012). Here, we postulate a simple conceptual model where the characteristics of resident vegetation help to explain the variance in invader performance at patch scale (Fig. 1). Invader performance could vary predictably from patch to patch as direct and indirect negative interactions (i.e., seed predation, competition) vary as a result of resident vegetation characteristics. In particular, differences regarding to resident plant cover, productivity, and growing season length might directly reduce invader performance through increasing competition strength (Grime 1979; Burke and Grime 1996; Chesson 2000; Davis et al. 2000). Also, favorable habitat conditions for consumers might indirectly reduce invasion through seed and seedling predation (Orrock et al. 2008; Garcia et al. 2011). As a consequence, patch identity might limit plant invasion by changing the niche opportunities for exotic invaders (dashed line in Fig. 1; Shea and Cheeson 2002). Superimposed on the mosaic of patches, disturbance should improve the performance of plant invaders by relaxing aerial and belowground negative interactions (Picket and White 1985; Burke and Grime 1996; D'Antonio et al. 1999; Davis et al. 2000; Jurena and Archer 2003) and also by eliminating refuge for consumers (Orrock et al. 2008; Garcia et al. 2011). The magnitude of invader performance improvement should be higher as disturbance erases more restrictive conditions for the invader (solid line in Fig. 1). Overall, how invader performance changes across different patch composition will improve our knowledge on community invasion and grassland encroachment.

In order to test this conceptual model, we evaluated the effect of patch identity on the establishment and growth of tree seedlings in two old-fields grasslands communities in an agricultural landscape of the Inland Pampa. *Gleditsia triacanthos* L. (hereafter named by genus) is one of the most common tree invaders in the region, especially in non cultivated lands (Ghersa et al. 2002). Previous studies have shown that grass competition is a biotic barrier against *Gleditsia* establishment and growth (Mazía et al. 2001, 2010; Chaneton et al. 2004). Here, we focus on seed predation, seedling

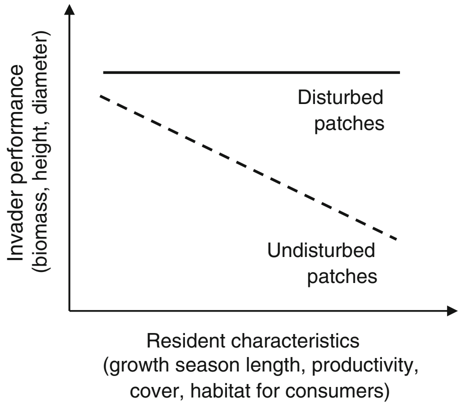

**Fig. 1** Predictions regarding woody establishment and growth in different patches along an increasing axis of growth season length, productivity, plant cover, and habitat for consumers. *Dashed* and *continuous line* show predictions for undisturbed and disturbed patches, respectively

emergence, survival and growth of *Gleditsia* in four different disturbed and undisturbed patch types. As resident vegetation, we selected monospecific patches of a forb (*Conium maculatum* L.) and three grasses (one annual: *Lolium multiflorum* Lam. and two perennial: *Cynodon dactylon* (L.) Pers. and *Festuca arundinacea* Schreb., hereinafter named by genus). In accordance with our conceptual model (Fig. 1), we predict that *Gleditsia* invasion should decrease from *Conium* through *Lolium* to *Cynodon* and *Festuca* (see species description in Materials and methods). We also predict that disturbances will enhance seedlings establishment and growth more for perennial grasses than for annual grass or forbs, as reflected in a significant patch identity × disturbance interaction (Fig. 1).

## Materials and methods

### Study system

The experiment was conducted at Estancia San Claudio, a farm owned by the University of Buenos Aires in Carlos Casares county, Buenos Aires Province, Argentina (35°53′ S; 61°12′ W). The climate is sub-humid, with mean temperatures 23.4 °C in January and 8.2 °C in July. Mean annual precipitation (1976–2009) was 1,090 mm. Soils are well drained typic Hapludols, with 2.5 % organic mater. The landscape comprises a mosaic of cultivated land, sown pastures, and old-fields grasslands (Tognetti et al. 2010). The experiment was replicated in two 4 ha sites located 4 km apart. One of them was formerly a pasture and the other was a crop field, both cultivated for more than 50 years and closed to agriculture and domestic cattle during the last 30 years. These plant communities are composed of a mix of annual and perennial species (Omacini et al. 1995; Tognetti et al. 2010). Early successional stages are dominated by annual forbs and grasses (Omacini et al. 1995) perennial grasses became dominant as succession proceeds although patches of annual species remain conspicuous (Tognetti et al. 2010). *Gleditsia* is one of the most abundant invasive tree in the region (Ghersa et al. 2002). Bud break starts in early spring (September) while ripe fruits fall during May, seedling recruitment occurs between November and February.

### Experimental setting

We selected four exotic species patch types (*Conium*, *Lolium*, *Cynodon*, or *Festuca*) which represent close to 45 % of total abundance in advanced old-field series (Tognetti et al. 2010). *Conium* is an annual cool season forb which form dense stands of ~1.8 m tall and produce copious seeds; *Lolium* is an annual cool season grass of ~0.8 m tall. Both species show a biomass peak in late spring (November) (Gibson 2009). We also selected two patches of perennial grasses, *Cynodon* and *Festuca*. The former is a warm season C4 grass of ~0.5 m tall with maximum biomass in late summer. This grass spreads clonally, and has abundant rhizomes and stolons (Gibson 2009). In turn, *Festuca* is a cool season perennial tussock grass of ~1.2 m, with two biomass peaks in late spring and early autumn (Gibson 2009).

On December 2009, three replicates were haphazardly selected for each patch type in both sites (24 patches in total). Species dominance was defined by having more than 90 % aerial cover for *Conium, Cynodon, and Festuca*, and >60 % in *Lolium* patches (Tognetti and Chaneton 2012). To reduce edge effect and ensure independence each patch was at least 16 $m^2$ in size and was separated by more than 20 m apart from other experimental patch. Within each patch we marked two circular 1 $m^2$ plots; disturbance was applied at random in one of the halves by cutting and removing all aboveground biomass. This treatment was maintained during two consecutive growing seasons (2009–2011) by removing all emerging plants (forbs and grasses). In total there were 48 experimental units assigned to four patch types and two disturbance levels (disturbed and undisturbed) replicated three times in each old-field.

We evaluated seed loss by rodent predation by placing 20 *Gleditsia* seeds in petri dishes (9 cm diameter) in each plot during two nights in March 2010 (autumn). Resident granivores are mostly small size native rodents (*Akodon azarae*) which readily consume *Gleditsia* seeds (Mazía et al. 2010; Busch et al. 2012). Tree recruitment from seeds was evaluated by adding 20 scarified seeds into 0.20 × 0.20 $m^2$ quadrats located in each plot (installed in December 2009). To evaluate seedling growth, three *Gleditsia* seedlings were transplanted into each circular plot (144 seedlings in total) in November 2009 (spring). Tree seedlings were grown from seeds collected within the study area. *Gleditsia* seeds were previously scarified to remove hard coats and were germinated in petri dishes placed in 20 °C chambers. Pregerminated seeds were individually sown in plug trays dividing in 56 $cm^3$ cells. Seedlings were grown during 7 weeks in unheated greenhouse placed on the University campus. Before being transplanted in the field, seedlings were placed outdoors under a reduced watering regime to reduce transplant shock (Kozlowsky et al. 1991). At the time of field transplant, seedling size was (mean ± SD): height 8.15 ± 1.1 cm; diameter 1.6 ± 0.14 mm.

### Data collection and statistical analysis

At the beginning of the experiment (December 2009), we characterized initial patch conditions in undisturbed and disturbed treatments by measuring resident plant biomass, light penetration, and gravimetric soil moisture. Plant biomass was measured within two 0.2 × 1.0 m strips placed in each patch type; harvested samples were sorted in dead and live biomass, dried (70 °C) and weighed. Light penetration was measured through the relationship between light at the soil surface and light incident above the canopy (PPFD μmol $m^{-2}$ $seg^{-1}$) with a 1 × 100 cm. photon flux bar (Cavadevices®, Buenos Aires, Argentina). We averaged two measures per patch in N–S and E–W direction to obtain one value per patch. Water content (%) was measured after drying a 0–15 cm soil sample at 105 °C.

Seed loss (%) was measured as the number of removed and broken (bitten) seeds after two nights of field exposition (see above). Tree recruitment from seeds was estimated by counting new emerged seedlings within each plot during two growing season (Dec. 2009–March 2010 and Dec. 2010–March 2011). Tree survival and growth (height and basal diameter) were measured at the same dates. Basal diameter and height were measured with hand caliber and ruler, respectively. The three seedling measures were averaged to obtain one data per sampling date in each plot. At the end of the experiment (March 2011), we harvested all remaining trees from each plot. Saplings were removed with a spade with the first 25 cm of soil to sample the roots, which were gently washed to remove soil. All plants were separated into above (leaves and stems) and belowground (crown and roots) components, dried (70 °C) and weighted for biomass determination.

Data analyses were carried out through linear mixed effects models performed in R v 2.9.0 (The R Foundation for Statistical Computing, 2009). This allowed us to model patch variance heterogeneity (instead of transforming the original data) and to account for temporal autocorrelation in consecutive plant measures (Zuur et al. 2009). On the one hand, count variables (seed predation and plant survival) were analyzed with general linear models with "logit" link in *lmer* function in "lme4" package (Crawley 2007). On the other, we used *lme* function in "nlme" for continuous variables. First, initial live, dead, and total biomass were analyzed using patch type as explanatory fixed variable, and sites as random blocks. Second, soil water content, light penetration, final tree biomass, height and diameter were modeled using patch type and disturbance as fixed effects and sites as random effects. Finally, growth rate (height, diameter, and height/diameter) were modeled including time as a random variable (Zuur et al. 2009). We account for non independence between consecutive sampling dates by assuming a first degree autocorrelation structure in the model (AR1 type, Zuur et al. 2009). We analyzed last sampling date separately as a measurement of final integrative effect of patch and disturbance on plant growth. Multiple comparisons among treatments were performed with Fisher-LSD test based on Wald test (Di Rienzo et al. 2011).

## Results

Initial total aboveground biomass differed substantially among patch type ($F_{3,19} = 4.47$, $P = 0.015$,

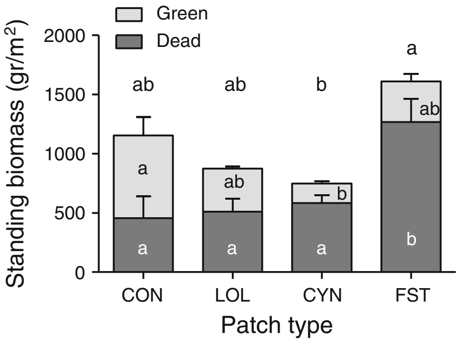

**Fig. 2** Total aboveground biomass in forb and grass patches at the beginning of the experiment (December 2009). *Conium maculatum* (CON), *Lolium multiflorum* (LOL), *Cynodon dactylis* (CYN), and *Festuca arundinacea* (FST). Harvested material was sorted into live (*gray bars*) and dead biomass (*black bars*). Different letters indicate significant differences ($P < 0.05$) within biomass components (*total, green* and *dead*, respectively). *Bars* show mean ± 1SE

Fig. 2). Total biomass in patches dominated by *Festuca* doubled that of *Cynodon* and *Lolium* patches, and was also 28 % higher than in *Conium* patches. These differences were mainly generated by higher accumulation of dead material in *Festuca* patches ($F_{3,19} = 5.06$, $P < 0.01$, Fig. 2). Live biomass was highest in *Conium* and lowest in *Cynodon* patches ($F_{3,19} = 5.53$, $P < 0.01$, Fig. 2). Disturbance significantly increased light penetration regardless of patch type (Disturbance: $F_{1,39} = 36.14$, $P < 0.001$, Fig. 3a). The effect of disturbance on soil water content varied among patches (Patch × Disturbance: $\mathrm{F}_{3,39}$: 6.39, $P < 0.005$); disturbance slightly reduced soil moisture (5 %) only in *Cynodon* patches, while there were no differences in soil moisture across intact patches (Fig. 3b).

Seed predation ranged between 15 and 80 % across disturbed and undisturbed patches (Fig. 4) and was nearly 80 % in *Conium* patches regardless of disturbance. The effect of disturbance on *Gleditsia* seeds removal varied among patch type (Patch × Disturbance: $\chi^2_3 = 68.48$, $P < 0.001$). While seed removal in *Conium* and *Lolium* was similar in undisturbed and disturbed patches, removal of resident vegetation drastically reduced seed predation in both *Cynodon* and *Festuca* patches (Fig. 4).

Tree seedling recruitment from added seeds was nil independent of disturbance and patch identity. Field observations revealed that 2 years after experimental setup, added seeds had completely disappeared from the sown quadrats, which suggest they were consumed by resident granivores. Only a few broken seeds remained on the soil with marks of consumption (Muschetto, *personal observation*). Neither patch type nor disturbance affected tree seedling survival 2 years

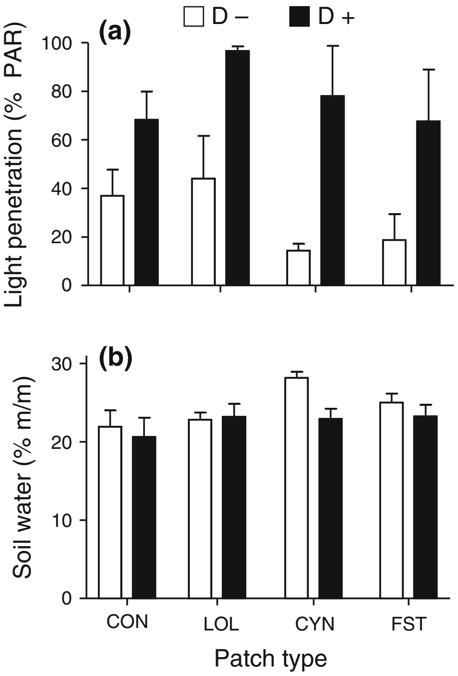

**Fig. 3** Light penetration (**a**) and soil water (**b**) in undisturbed (D−; *open bars*) and disturbed (D+; *black bars*) patches of four species [*C. maculatum* (CON), *L. multiflorum* (LOL), *C. dactylis* (CYN), and *F. arundinacea* (FST)]. Measures were taken at the beginning of the experiment (December 2009). *Bars* show mean ± 1SE

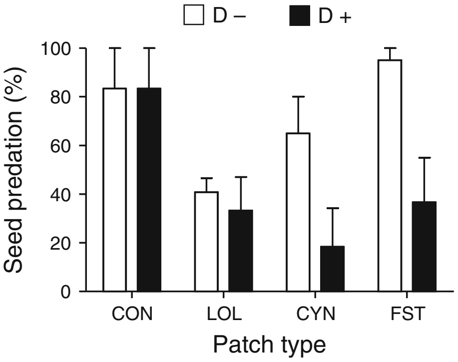

**Fig. 4** Total seed predation in intact (*open bars*) and disturbed (*black bars*) patches of four species (see Fig. 2 for details). Seeds were considered as predated when broken or removed from petri dish after two nights in the field (initially 20 seeds). *Bars* show mean ± 1SE

**Table 1** Results for the mixed effect model for height (cm) and basal diameter (mm) of *Gleditisia* saplings growing in four patch types under two disturbance levels

| | df | Year 1 | | | | Year 2 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Height | | Basal diameter | | Height | | Basal diameter | |
| | | F | *P* value | F | *P* value | F | *P* value | F | *P* value |
| Site | 1, 39 | 1.05 | 0.313 | 2.24 | 0.142 | 11.79 | <0.001 | 0.24 | 0.622 |
| Patch (P) | 3, 39 | 0.39 | 0.756 | 0.22 | 0.881 | 0.26 | 0.853 | 6.21 | 0.001 |
| Disturbance (D) | 1, 39 | 1.02 | 0.318 | 0.02 | 0.896 | 9.74 | 0.003 | 21.05 | <0.001 |
| P × D | 1, 39 | 0.04 | 0.988 | 1.02 | 0.392 | 0.52 | 0.672 | 0.46 | 0.711 |
| Time (T) | 1, 40 | 68.57 | <0.001 | 127.47 | <0.001 | 73.56 | <0.001 | 78.78 | <0.001 |
| P × T | 3, 40 | 3.13 | 0.035 | 3.73 | 0.018 | 4.21 | 0.011 | 4.44 | 0.008 |
| D × T | 1, 40 | 0.89 | 0.349 | 12.28 | 0.001 | 3.97 | 0.053 | 4.77 | 0.035 |
| P × D × T | 3, 40 | 0.17 | 0.911 | 0.82 | 0.490 | 1.81 | 0.160 | 0.85 | 0.474 |

Tree seedlings were measured at the beginning and at the end of two growing seasons (December 2009 to March 2010 and December 2010 to March 2011)

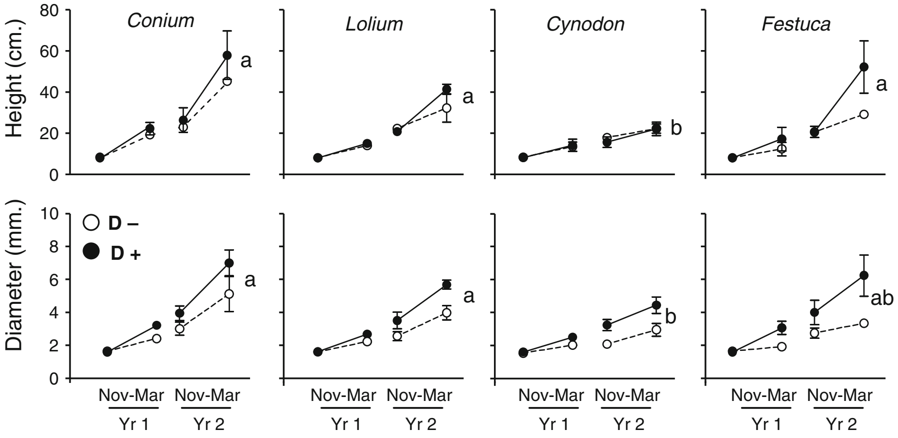

**Fig. 5** Tree seedling height (*upper panels*) and basal diameter (*lower panels*) during two growing season (November–March) in undisturbed (*open symbols*) and disturbed patches (*black symbols*) of four species (*Conium*, *Lolium*, *Cynodon*, and *Festuca*). Different letters indicate significant differences among patch types for the last sampling date ($P < 0.05$). *Symbols* show mean ± 1SE

after planting, which was nearly 60 % throughout the experiment (Patch effect: $X^2 = 4.56$, $P > 0.2$; Disturbance effect $X^2 = 0.28$, $P > 0.6$, Patch × Disturbance: $X^2 = 1.07$, $P > 0.78$).

Tree seedling growth was affected by patch identity and disturbance during both the 2009–2010 and 2010–2011 growing seasons (Table 1; Fig. 5). On average, tree height increased from 8 to 16 cm and from 20 to 40 cm during the first and the second year of the experiment, respectively. During the first season tree height growth in *Conium* exceeded that recorded in grass patches (Patch × Time: $P = 0.035$, Fig. 5), while at the second growing season trees in *Conium*, *Lolium*, and *Festuca* were taller than those in the *Cynodon* (Patch × Time $P = 0.011$, Fig. 5). Irrespective of patch identity, disturbance increased tree height growth during the second year of the experiment (Table 1). Also, disturbance positively affected tree basal diameter growth during both study seasons (Disturbance × Time, Table 1). The first growing season basal diameter increased from 0.5 to 1.27 mm in intact and disturbed patches, respectively, while in the second year the increase was 1.2 and 2.16 mm. Patch identity differentially affected diameter growth during the first and the second growing season (Patch × Time, Table 1), while *Conium* patches showed the highest diameter growth (1.20 and 2.58 mm first and second year, respectively), *Cynodon* showed the lowest diameter increase (0.69 and 1.03 mm) and *Lolium* and *Festuca* showed intermediate values (0.85 and 1.79 mm; 0.87 and 1.42 mm, respectively).

Disturbance and patch identity both affected final shoot and root tree biomass but did not show a significant interaction effect (Fig. 6; Table 2). The highest shoot and root biomass was found in *Conium* patches and the lowest values were found in *Cynodon* whereas sapling biomass was intermediate in *Lolium* and *Festuca*. On average disturbance slightly increased shoot and root biomass; however, this effect was more pronounced for roots than for shoots in perennial patches and, therefore, the shoot: root ratio of *Gleditsia* decreased in *Cynodon* and *Festuca* patches (Patch: $P = 0.028$, Disturbance: $P < 0.001$, Patch × Disturbance: ns; Table 2; Fig. 6).

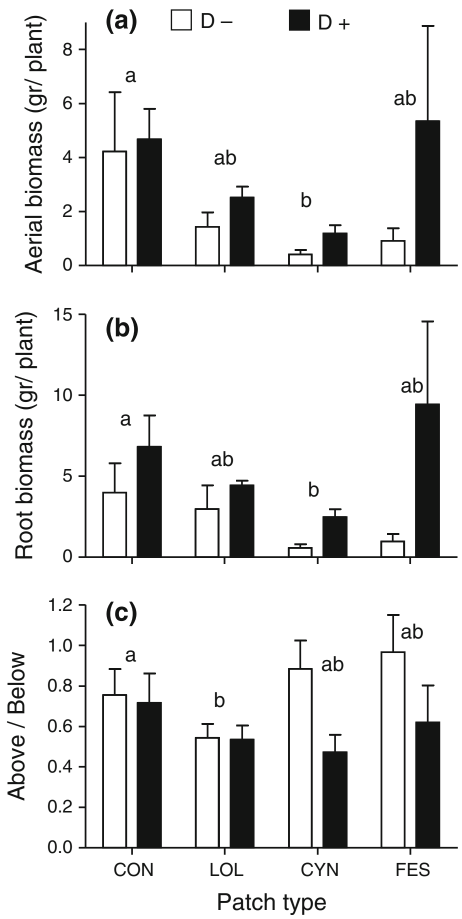

**Fig. 6** Tree seedlings biomass at the end of the experiment (March 2011). **a** Leaves and shoots, **b** roots, **c** aerial/roots for plants growing in four patch types (see Fig. 2 for details). *Bars* show mean ± 1SE. Different letters indicate significant differences among patch types ($P < 0.05$)

## Discussion

Woody encroachment in grasslands involves the successful establishment and spread of woody individuals over a spatially heterogeneous herbaceous community. The present study revealed that patch identity played a significant influence on resistance to woody establishment in grasslands communities. We found three important aspects of the process of tree invasion which are related to the identity of the resident vegetation. First, in relation to propagule availability, we found that seed removal beneath intact vegetation was an important biotic filter to woody establishment, whereas disturbances facilitated seed survival in patches of perennial grasses. Second, grass competition substantially reduced tree growth within C4 grass patches, providing evidence of strong tree growth variability related to patch identity. Finally, we found that disturbance improved tree seedling growth and final biomass regardless of patch identity. Taken together all these results imply that spatial heterogeneity in patch composition creates a changing scenario for woody encroachment, where patches would offer different opportunities or generate particular limitations to tree species establishment.

Community biotic interactions, including predation and competition, constitute one of the main barriers to plant invasion (Williamson 1996; Levine and D'Antonio 1999; Levine et al. 2004). The importance of granivory as a source of resistance to invasion was shown in prior studies focusing on herbaceous (Maron and Kauffman 2006; Murillo et al. 2007; Pearson et al. 2011) and woody invaders (Weltzin et al. 1997; Mazía et al. 2010; Busch et al. 2012). However, those studies did not account for the spatial heterogeneity of seed predation in response to plant community patchiness (Garcia et al. 2011). Here, we found that seed consumption by native rodents acted as the first filter to woody establishment. In a short term removal experiment (two nights), both disturbance and patch identity influenced tree seed persistence, whereas in the longer term (2 years) all seeds incorporated in each plot failed to establish. Compared to previous works, where seed addition rate was similar to the present study (Mazía et al. 2001; 2010), our results suggest that adding ~80 seeds $m^2$ was not sufficient to overcome the pressure of resident granivores. However, in the longer term, under seed scarcity scenario like the

**Table 2** Results for the mixed effect model for above (*leaves* + *shoots*) and belowground (*roots*) biomass of *Gleditisia* saplings growing in four patch types under two disturbance levels

| | df | Above | | Belowground | | Above/below | |
|---|---|---|---|---|---|---|---|
| | | F | *P* value | F | *P* value | F | *P* value |
| Patch | 3, 39 | 5.99 | 0.002 | 10.82 | <0.001 | 3.34 | 0.028 |
| Disturbance | 1, 39 | 8.10 | 0.007 | 19.87 | <0.001 | 14.57 | <0.001 |
| P × D | 3, 39 | 1.08 | 0.362 | 1.18 | 0.327 | 1.46 | 0.240 |

context of our experiment, seed removal by rodents was not affected by patch identity.

Interestingly, we found that seed removal was affected by disturbance only in *Festuca* and *Cynodon* patches (significant patch × disturbance interaction). This evidence suggest that gaps within a closed and continuous matrix of grasses (*Festuca* or *Cynodon*) were highly exposed microsites compared to gaps placed in a more open matrix of vegetation (*Conium* or *Lolium*). Structural differences between patches were evident through differences in light penetration between disturbed and undisturbed patches of *Conium* and *Lolium* with respect to such differences in *Cynodon* and *Festuca* patches (Fig. 2). Overall if rodents perceive a differential risk among vegetation gaps embedded in different patch types, then the surrounding matrix composition would become critical to the survival of seeds arriving in disturbated gaps (Garcia et al. 2011). While newly established populations could be more seed than microsite limited (Turnbull et al. 2000; Clark et al. 2007; Simberloff 2009), our short term experiment stresses that microsites differences (patch identity and disturbance) may indirectly modify seed availability through changes in consumers behavior (Orrock et al. 2008; Mazía et al. 2010).

Patch identity was an important source of difference in tree growth, which on average varied up to 80 % between *Conium* and *Cynodon* patches. The warm C4 grass *Cynodon* was the strongest competitor in limiting seedling diameter, height, and final biomass (above and belowground). Basal diameter is a trait positively associated with competitive ability and root biomass of tree seedlings. Besides, individuals growing slowly are more exposed to risks than those growing fast (Kozlowsky et al. 1991; Archibald and Bond 2003). Therefore, it is plausible that tree seedlings growing within *Cynodon* patches could have scarce opportunities of medium term survival. Consistent with our finding, few tree seedlings survive within a native grassland dominated by C4 grasses, whereas tree seedling establishment and growth within an old-field dominated by C3 grasses was successful (Chaneton et al. 2004).

While we predicted that opportunities to *Gleditsia* establishment would be lower in *Festuca* than in *Cynodon* patches, our results show that the worst tree seedling performance was in *Cynodon* patches. It is possible that rather than the factors we had postulated as most important (Fig. 1), the phenological niche overlap between resident vegetation and invader species was more relevant in limiting invader performance (Chesson 2000; Wilsey et al. 2011; Tognetti and Chaneton 2012). Although our study did not reveal which specific mechanisms were involved in the differential growth rate between patches, it is known that synchronic demand for limited resources may affect performance of competing species (Verdú et al. 2012). In this regard, invasion criterion states that stabilizing (e.g., phenological differences) and/or equalizing (e.g., disturbance) forces may reduce competitive exclusion and lead to plant coexistence (Chesson 2000), at least in early invasion stages (see Levine et al. 2004). With this premise, synchrony between C4 grasses and deciduous trees might be an important aspect of patch identity accounting for limiting woody invasion in grasslands (Bond 2008).

Unsurprisingly, disturbance enhanced tree growth, but this increase in growth was independent of the patch identity. These results agreed with others studies which showed that grass cover is one of the principal barriers in lowering woody encroachment (Brown and Archer 1989; O'Connors 1995; Scholes and Archer 1997; Van Auken 2000; Riginos and Young 2007; Riginos 2009; Grellier et al. 2012). In assuming that disturbance would erase patch differences, we expected a significant patch type x disturbance interaction (Fig. 1). Although our results did not strongly confirm such expectation, seedlings growth in disturbed patches showed high variability. In particular disturbance in *Cynodon* patches did not substantially enhance tree seedling performance (Fig. 5). Similarly, Tognetti and Chaneton (2012) found that the effect of disturbance on the establishment of native grasses also depended on patch identity. Overall, it is possible that gaps in the vicinity of highly productive grasses such as *Cynodon* or *Festuca* (Tognetti and Chaneton 2012) have the potential to diminish the otherwise positive effect of disturbance on seedling growth through re-colonizing the space from neighborhood areas (Riginos 2009). Alternatively, below ground interactions might still play an important role after disturbance (Jurena and Archer 2003; Orr et al. 2005; Rudgers and Orr 2009).

In spite of the observed differences in sapling growth, tree seedling survival was homogeneous among patch types and disturbance treatment. On the one hand, our results highlight that niche requirements for growth were more restrictive than those for survival (Johnstone 1986; Hall et al. 1992). On the other, it is possible that added seedlings were beyond some critical threshold which reinforced their chances for survival (Facelli and Leon 1986; Chaneton et al. 2004; Mazía et al. 2010). However, given our results related to the effect of patch identity on tree growth, we suggest that to maintain perennial grass cover could help to diminish the chances of woody survival, as suggested by the low seedling performance recorded in undisturbed *Cynodon* and *Festuca* patches (Figs. 5, 6; Cochard and Edwards 2011; Grellier et al. 2012).

In conclusion, the results presented here highlight that community resistance or susceptibility to woody invasion in grasslands, more than representing a static community attribute represent a variable scenario which varies according to the spatial and temporal changes in the matrix of monospecific patches. We found high variation in tree growth among patches and disturbance treatments; therefore, community generates a changing scenario to plant invasion which might imply that intensity of plant competition, facilitation, or other indirect interactions change in time and space (Davis et al. 2000) generating different niche opportunities (Shea and Cheeson 2002). Under the scenario of increasing woody encroachment, which implies an increase in tree propagule availability (Chaneton et al. 2012), patch identity might play a substantial role in driving the patterns of tree invasion in old-field communities. Our results showed that exotic-dominated grasslands (Tognetti et al. 2010) created a heterogeneous barrier to successful tree establishment. Consequently, understanding the role of spatial vegetation heterogeneity would be crucial to devise management strategies for slowing exotic tree invasion.

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